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Clauss, Marcus ; Hofmann, R R ; Streich, W J ; Fickel, J ; Hummel, J

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# Higher masseter muscle mass in grazing than in browsing ruminants

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**Abstract** Using cranoskeletal measurements, several studies have generated evidence that grazing ruminants have a more pronounced mastication apparatus, in terms of muscle insertion areas and protuberances, than browsing ruminants, with the resulting hypothesis that grazers should have larger, heavier chewing muscles than browsers. However, the only investigation of this so far [Axmacher and Hofmann (J Zool 215:463–473, 1988)] did not find differences between ruminant feeding types in the masseter muscle mass of 22 species. Here, we expand the dataset to 48 ruminant species. Regardless of phylogenetic control in the statistical treatment, there was a significant positive correlation of body mass and masseter mass, and also a significant association between percent grass in the natural diet and masseter mass. The results support the concept that ruminant species that ingest more grass have relatively larger masseter muscles, possibly indicating an increased require-

ment to overcome the resistance of grass forage. The comparative chewing resistance of different forage classes may represent a rewarding field of ecophysiological research.

**Keywords** Masseter · Phylogeny · Grazer · Browser · Morphology

## Introduction

One of the key assumptions in the investigations of differences between browsing and grazing ungulates is that grasses require greater masticatory forces for a similar degree of functional particle size reduction than browse (e.g. Turnbull 1970; Stöckmann 1979; Solounias and Dawson-Saunders 1988; Clauss et al. 2008). This concept actually did not originate from comparative investigations of plant properties, but from comparative anatomical observations that pointed to a stronger masticatory apparatus in grazing ruminants or ungulates (Turnbull 1970; Ramisch 1978; Stöckmann 1979; Kiplel 1981; Axmacher and Hofmann 1988; Sasaki et al. 2001; Endo et al. 2002). A number of studies have shown that anatomical measurements related to the masticatory muscles, such as osseous muscle insertion areas or canals for nerves supplying the muscles (Solounias and Dawson-Saunders 1988; Janis 1990; Solounias et al. 1995; Solounias and Moelleken 1999; Mendoza et al. 2002; Mendoza and Palmqvist 2006), can help distinguish grazing and browsing ruminants.

However, the only study to directly measure masseter muscle mass in ruminants (Axmacher and Hofmann 1988) found no difference between the feeding types. This study was limited to 22 species examined. Therefore, we assembled a larger data set (48 ruminant species) with more taxonomic groups (giraffidae, cervidae, bovidae) to more

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carefully examine the relationship between masseter muscle mass and feeding style.

## Materials and methods

Animals were obtained over the years from hunting operations in Germany, Austria, Switzerland, Finland, Canada, Botswana, Namibia and South Africa, and from European zoological gardens. Consistency in method was guaranteed by the fact that the data were mainly generated by one of the authors (R. R. Hofmann), with a few additions by M. Clauss. Additional data were available for two tragulid species (Endo et al. 2002; corrected by one decimal point for an evident typographical error). Body mass was measured directly before dissection of the animals. Each pair of masseters was weighed to  $\pm 0.05$  g on electronic scales. As the masseter muscle mass in domestic cattle was shown to be independent from the feeding regime (Nakamura et al. 2007), masseter mass data from both free-ranging and captive animals were combined in this study. The average body mass and masseter mass measurements for the individual ruminant species are listed in Table 1.

The unpublished dataset of R. R. Hofmann contains data on more animal species than those given here (cf. Hofmann et al. 2008). However, for a certain subset of animals, body mass had not been determined by weighing, but by using the masseter mass as a surrogate measure, following the suggestion of Axmacher and Hofmann (1988). These data were excluded from the current analysis.

Animals were allocated to feeding type categories [browser (BR), intermediate feeder (IM), grazer (GR)] using the classification of Hofmann (1988), with additional information from more recent publications (Hofmann 1991, 1999; Hofmann et al. 1995). The percentage of grass in the natural diet (%grass) was used to characterize species on a continuous scale; the bulk of the respective data was taken from Van Wieren (1996) and the data collection that formed the basis of Owen-Smith (1997) (data kindly provided by the author), which were supplemented by several other publications (Table 1); whenever seasonal data were available, the %grass used to characterise a species represents the mean of the values from different seasons. These data have been collated using a variety of sources and methods, a problem shared by most comparative analyses performed at the inter-specific level.

Relationships among species were inferred from a phylogenetic tree based on the complete mitochondrial cytochrome *b* gene. Respective DNA sequences were available from GenBank (<http://www.ncbi.nlm.nih.gov>) for all ruminant species investigated. Sequences were aligned using ClustalX (Thompson et al. 1997), visually controlled and trimmed to identical lengths (1,143 bp). To select the

best-fitting nucleotide substitution model for the data, a combination of the software packages Paup\* (version 4.b10; Swofford 2002) and Modeltest (version 3.7; Posada and Crandall 1998) was used. Analysis was based on a hierarchical likelihood ratio test approach implemented in Modeltest. The model selected was the general time-reversible (GTR) model (Lanave et al. 1984; Tavaré 1986) with an allowance both for invariant sites (*I*) and a gamma (*G*) distribution shape parameter ( $\alpha$ ) for among-site rate variation (GTR + *I* + *G*) (Rodriguez et al. 1990). The nucleotide substitution rate matrix for the GTR + *I* + *G* model was likewise calculated using Modeltest. Parameter values for the model selected were:  $-\ln L = 15642.5273$ ,  $I = 0.4613$ , and  $\alpha = 0.8093$  (eight gamma rate categories). The phylogenetic reconstruction based on these parameters was then performed using the maximum likelihood method implemented in TreePuzzle (version 5.2; Schmidt et al. 2002). Support for nodes was assessed by a reliability percentage after 100,000 quartet puzzling steps; only nodes with more than 50% support were retained. The resulting tree is displayed in Fig. 1. The basal polytomy for familial relationships (Bovidae, Cervidae and Giraffidae) was resolved assuming it to be a soft polytomy (Purvis and Garland 1993). In order to meet the input requirements for the phylogenetic analysis implemented in the COMPARE 4.6 program (Martins 2004), we resolved the remaining polytomies to full tree dichotomy by introducing extreme short branch lengths ( $l = 0.00001$ ) at multifurcating nodes. Taxa grouping in the bifurcating process followed the phylogenies proposed by Pitra et al. (2004) for Cervidae and by Fernandez and Vrba (2005) for all other taxa.

The subject of the comparative analyses were individual species, each characterized by its respective mean masseter mass as described above. In order to achieve normal data distribution, both masseter mass and body mass data were ln transformed for all calculations. Following earlier studies (Pérez-Barbería et al. 2001; Clauss et al. 2006; Hofmann et al. 2008), statistical analyses were performed with and without accounting for phylogeny, to test for the validity of a general, functional hypothesis, and to then discriminate between convergent adaptation and adaptation by descent. Linear models were used to compare categorical feeding types (BR, IM, GR) and to investigate the interrelations between body mass, feeding type (as %grass), and masseter mass according to the equation  $\ln(\text{masseter muscle mass}) = a + b \ln(\text{BM})$  resp.  $\ln(\text{masseter muscle mass}) = a + b \ln(\text{BM}) + c \% \text{grass}$ . In order to additionally include phylogenetic information, we used the phylogenetic generalized least-squares approach (Martins and Hansen 1997; Rohlf 2001) in which a well-developed standard statistical method was extended to enable the inclusion of interdependencies among species due to the evolutionary process. In order to test the robustness of the results, the comparative analysis

**Table 1** Number of males (*M*), females (*F*) and individuals of unknown sex (*UK*) investigated for this study and their origin [free-range (*FR*), semi-free-range (*SFR*), zoo (*Z*)], mean ( $\pm$  SD) body mass (kg) and masseter muscle mass (g) measurements of individuals of differentruminant species [of different feeding type: browser (*BR*), intermediate feeder (*IM*), grazer (*GR*)], as well as the percentage of grass in the species' natural diet<sup>a</sup> (%*Grass*) according to literature sources

Species		<i>n</i> (M, F, UK)	Origin	Body mass (kg)	Masseter mass (g)	%Grass	Source <sup>b</sup>
<i>Addax nasomaculatus</i>	GR	3, 3, 0	Z	83.8 $\pm$ 10.5	262.2 $\pm$ 27.3	80	3
<i>Alcelaphus buselaphus</i>	GR	1, 0, 0	FR	217.5	461.0	97	2
<i>Alces alces</i>	BR	1, 1, 4	FR	179.7 $\pm$ 56.0	367.0 $\pm$ 82.2	2	1
<i>Antidorcas marsupialis</i>	IM	4, 1, 0	FR	43.5 $\pm$ 5.6	89.2 $\pm$ 9.7	30	4
<i>Antilocapra americana</i>	IM	1, 1, 0	FR	45.0 $\pm$ 2.8	86.4 $\pm$ 6.4	15	1
<i>Antilope cervicapra</i>	GR	1, 0, 0	SFR	35.0	89.5	75	1
<i>Axis axis</i>	IM	1, 1, 0	SFR	50.5 $\pm$ 9.2	94.7 $\pm$ 27.8	70	1
<i>Axis porcinus</i>	IM	2, 1, 0	SFR	49.4 $\pm$ 13.4	100.6 $\pm$ 8.1	50	5
<i>Beatragus hunteri</i>	GR	1, 0, 0	FR	130.0	287.0	90	6
<i>Bos javanicus</i>	GR	0, 1, 0	Z	600.0	996.0	80	est.
<i>Boselaphus tragocamelus</i>	IM	1, 0, 0	SFR	88.0	179.0	60	2
<i>Capra hircus</i>	IM	0, 0, 2	Z	33.5 $\pm$ 2.1	76.3 $\pm$ 0.2	28	1
<i>Capreolus capreolus</i>	BR	1, 0, 2	FR	26.3 $\pm$ 3.2	44.2 $\pm$ 11.6	9	1
<i>Cephalophus harveyi</i>	BR	1, 0, 0	FR	8.3	21.8	1	3
<i>Cephalophus monticola</i>	BR	0, 1, 0	FR	4.0	9.2	1	7
<i>Cervus elaphus</i>	IM	1, 0, 0	Z	85.0	177.2	47	1
<i>Cervus nippon</i>	IM	3, 1, 0	FR/SFR	34.8 $\pm$ 13.8	64.4 $\pm$ 25.0	50	1
<i>Dama dama</i>	IM	2, 5, 0	FR	61.8 $\pm$ 19.6	92.8 $\pm$ 31.8	46	1
<i>Damaliscus pygargus</i>	GR	1, 0, 0	FR	83.0	196.0	100	9
<i>Elaphurus davidianus</i>	GR	1, 0, 0	SFR	190.6	420.3	75	10
<i>Gazella subgutturosa</i>	IM	1, 0, 0	Z	13.1	25.0	50	11
<i>Giraffa camelopardalis</i>	BR	0, 1, 0	Z	800.0	1026.4	0	2
<i>Hippotragus niger</i>	GR	1, 1, 0	FR	177.5 $\pm$ 81.3	358.0 $\pm$ 166.9	93	12
<i>Hydropotes inermis</i>	IM	2, 4, 0	SFR	12.7 $\pm$ 1.4	26.2 $\pm$ 4.4	50	10
<i>Kobus leche</i>	GR	1, 0, 0	Z	72.0	149.2	95	3
<i>Madoqua guentheri</i>	BR	2, 2, 0	FR	4.4 $\pm$ 0.2	9.6 $\pm$ 1.9	5	14
<i>Mazama americana</i>	BR	3, 3, 0	FR	14.2 $\pm$ 5.4	27.5 $\pm$ 9.3	1	15
<i>Muntiacus reevesi</i>	BR	0, 0, 2	SFR	12.7 $\pm$ 1.6	26.4 $\pm$ 1.9	10	1
<i>Neotragus moschatus</i>	BR	1, 1, 1	FR	3.7 $\pm$ 0.2	9.2 $\pm$ 1.5	0	8
<i>Odocoileus virginianus</i>	BR	1, 1, 0	FR	66.1 $\pm$ 27.6	94.4 $\pm$ 24.6	9	1
<i>Oryx gazella</i>	GR	1, 0, 0	FR	192.1	461.0	82	2
<i>Oryx leucoryx</i>	GR	0, 1, 0	Z	75.0	228.0	75	3
<i>Ourebia ourebi</i>	GR	0, 1, 0	FR	20.0	37.5	49	2
<i>Ovis ammon domesticus</i>	GR	0, 0, 1	Z	32.0	80.0	50	1
<i>Ovis ammon musimon</i>	GR	1, 0, 0	SFR	55.0	143.2	69	16
<i>Pelea capreolus</i>	BR	2, 0, 0	FR	16.3 $\pm$ 1.8	31.8 $\pm$ 2.3	7	17
<i>Raphicercus campestris</i>	BR	0, 0, 1	FR	10.7	15.3	10	1
<i>Raphicercus melanotis</i>	IM	1, 0, 0	FR	9.1	16.5	30	3
<i>Redunca redunca</i>	GR	0, 1, 0	FR	21.9	54.0	80	1
<i>Rupicapra rupicapra</i>	IM	2, 3, 0	FR	24.3 $\pm$ 7.4	58.9 $\pm$ 4.0	74	1
<i>Sylvicapra grimmia</i>	BR	1, 0, 0	FR	13.0	30.3	5	2
<i>Syncerus caffer</i>	GR	1, 0, 0	FR	650.0	1308.0	90	1
<i>Tragelaphus angasi</i>	BR	2, 3, 0	FR/Z	75.9 $\pm$ 38.3	147.6 $\pm$ 71.3	20	18
<i>Tragelaphus imberbis</i>	BR	2, 0, 0	Z	46.5 $\pm$ 5.0	94.0 $\pm$ 18.9	10	2

**Table 1** continued

Species	<i>n</i> (M, F, UK)		Origin	Body mass (kg)	Masseter mass (g)	%Grass	Source <sup>b</sup>
<i>Tragelaphus speki</i>	BR	2, 0, 0	Z	55.0 ± 9.9	101.3 ± 37.1	68	19
<i>Tragelaphus strepsiceros</i>	BR	1, 1, 0	FR/Z	127.5 ± 88.4	238.5 ± 139.3	5	1
<i>Tragulus javanicus</i> <sup>c</sup>	BR	2, 1, 0	FR	1.3 ± 0.1	3.8 ± 0.9	0	20
<i>Tragulus napu</i> <sup>c</sup>	BR	0, 2, 0	Z	2.7 ± 0.2	6.1 ± 0.9	0	20

<sup>a</sup> Diets of animals measured for this study were generally not recorded. FR animals may be assumed to have foraged naturally; SFR animals were kept on extensive pastures at Whipsnade Wild Animal Park, UK; diets of Z animals were not recorded except for *A. nasomaculatus* (grass hay, wheat bran), *B. javanicus* (fresh grass, grass hay, beet pulp), *G. subgutturosa* (fresh grass, grass hay, pelleted mixed feed, vegetables), *G. camelopardalis* (lucerne hay, browse, pelleted mixed feed, vegetables), *O. leucoryx* (grass hay, pelleted mixed feed, vegetables)

<sup>b</sup> Literature sources for percent grass: 1 (Van Wieren 1996), 2 (Owen-Smith 1997), 3 (Gagnon and Chew 2000), 4 (Bigalke 1972), 5 (Dhungel and O'Gara 1991), 6 (Andanje and Ottichilo 1999), 7 (Dubost 1984), 8 (Heinichen 1972), 9 (Du Plessis 1972), 10 (Geist 1999), 11 (Heptner et al. 1989), 12 (Grobler 1974), 14 (Hofmann and Stewart 1972), 15 (Branan et al. 1985), 16 (Stubbe 1971), 17 (Ferreira and Bigalke 1987), 18 (Lobao Tello and van Gelder 1975), 19 (Owen 1970), 20 (Nordin 1978); *Est.* estimated as in Clauss et al. (2006)

<sup>c</sup> Data from Endo et al. (2002)

was performed for both a set of phylogenetic trees involving branch lengths (tree 1) and another set with equal branch lengths (tree 2). As there were no relevant differences in the results, only the tests using tree 1 are given here. In order to visualize the correlation between %grass and masseter mass after body mass had been controlled for, the residuals of the masseter measurements were plotted against %grass. The residuals were calculated using allometric regression with body mass according to the equation  $\ln(\text{masseter muscle mass}) = a + b \ln(\text{BM})$  and served just for the purpose of demonstrating the relationship in two dimensions. The COMPARE 4.6 program (Martins 2004) served for the phylogenetically controlled calculations. The other statistical calculations were performed with the SPSS 12.0 software (SPSS, Chicago, Ill.). The significance level was set to  $\alpha = 0.05$ .

## Results

Averaged across all species, masseter mass represented 0.212% of the body mass, with a median of 0.206 and a range of 0.128–0.313 (95% confidence interval for the mean 0.201–0.223). In general, the masseter muscle mass scaled nearly isometrically to body mass. The regression between masseter mass and body mass according to the equation,  $\ln(\text{masseter muscle mass}) = a + b \ln(\text{BM})$ , was highly significant (without phylogeny,  $R^2 = 0.983$ ,  $P < 0.001$ ; including phylogeny,  $R^2 = 0.983$ ,  $P = 0.001$ ), and an isometric scaling in the equivalent power equation,  $\text{masseter muscle mass} = e^a \text{BM}^b$  (exponent  $b = 1.0$ ), was just excluded by the 95% confidence interval (without phylogeny, 0.925–0.999; including phylogeny, 0.921–0.996).

The relationship between BM and the mass of the masseter muscle differed among the three categorical feeding types (Fig. 2). The slopes of the regression lines for BR, IM, and GR differed ( $P = 0.038$ ). When IM were excluded, slopes

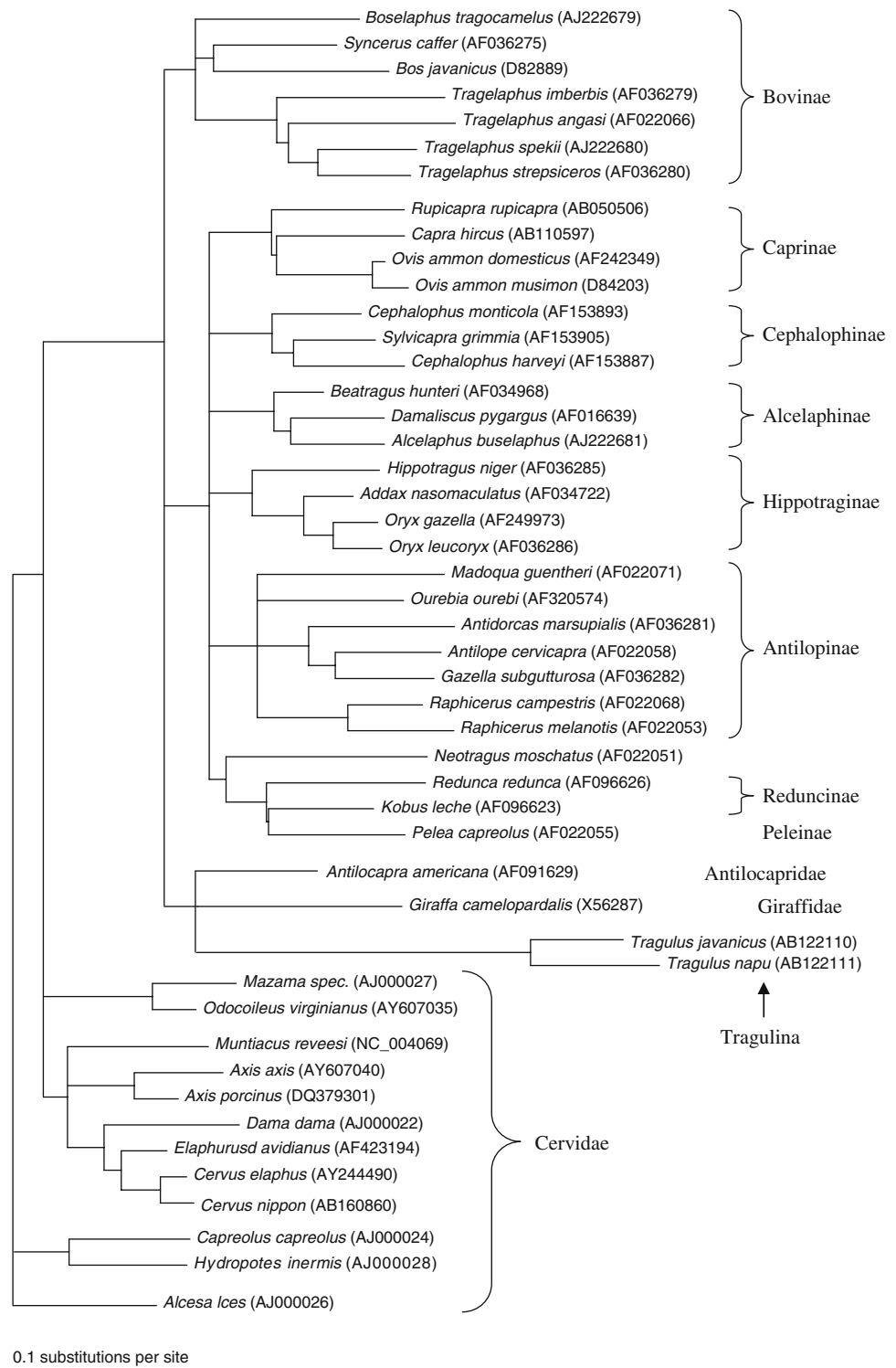
for BR and GR did not differ significantly ( $P = 0.592$ ), and both significant effects of body mass ( $P < 0.001$ ) and feeding type occurred (i.e. a significant difference between BR and GR,  $P < 0.001$ ). When the three categorical feeding types were compared including phylogeny, there was also a significant difference in slopes ( $P = 0.049$ ). After excluding the IM, there was no significant difference between the slopes ( $P = 0.539$ ), and again, both body mass ( $P < 0.001$ ) and feeding type (i.e. BR vs. GR,  $P < 0.001$ ) showed significant effects.

Regardless of whether phylogeny was accounted for or not, both body mass (Fig. 2) and %grass in the natural diet (Fig. 3) showed a significant, positive correlation to the masseter muscle mass according to the equation,  $\ln(\text{masseter muscle mass}) = a + b \ln(\text{BM}) + c \% \text{grass}$  [without phylogeny,  $R^2 = 0.987$ ,  $P(R^2) < 0.001$ ,  $a = 0.892$ ,  $b = 0.922$ ,  $P(b) < 0.001$ ,  $c = 0.003$ ,  $P(c) < 0.001$ ; including phylogeny,  $R^2 = 0.986$ ,  $P(R^2) < 0.001$ ,  $a = 0.882$ ,  $b = 0.926$ ,  $P(b) < 0.001$ ,  $c = 0.003$ ,  $P(c) = 0.003$ ].

## Discussion

Using the traditional, categorical feeding types, we found a significant difference in masseter mass between grazing and browsing ruminants that was independent of body mass and phylogeny. Differences in slopes have been encountered repeatedly in comparisons of categorical feeding types (see Table 3.5 in Clauss et al. 2008); the use of a continuous variable such as %grass prevents this problem and allowed, in this case, the use of the full dataset of 48 species to corroborate the result. In preparing categorical tests, the classification of individual ruminant species into feeding types is problematic, because no standardized cut-off points exist for the transitions between intermediate feeders and the two extreme feeding types. This problem had already been

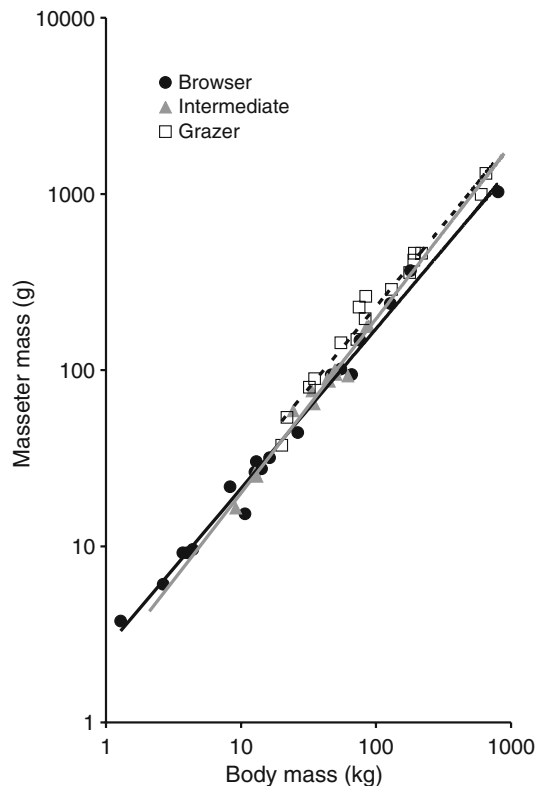
**Fig. 1** Fifty percent majority rule maximum likelihood tree (100,000 puzzling steps, log  $L = -188,62.584$ ), depicting the phylogenetic relationships among complete mitochondrial cytochrome *b* sequences from 48 ruminant taxa as used in the phylogenetically controlled statistics in this study (accession codes from GenBank (<http://www.ncbi.nlm.nih.gov>))



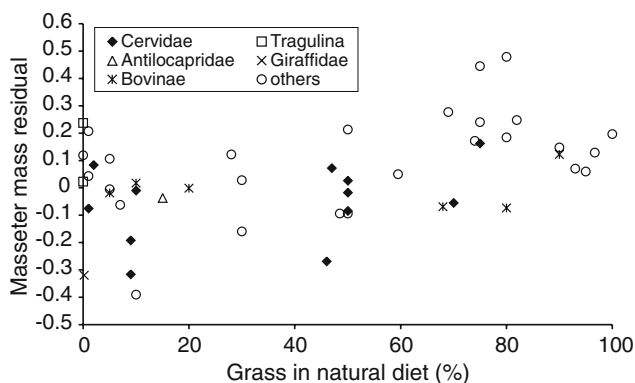
indicated by Gordon and Illius (1994) who found evidence supporting the hypotheses of Hofmann (1989) when using Hofmann's own categorical classification but could not support these hypotheses with a classification of their own. Actually, the practice of grouping species into feeding type categories has not been consistent even within research groups over time (discussed in Clauss et al. 2008). There-

fore, the use of quantitative data on the proportion of grass in the natural diet, rather than a categorical classification, has been proposed as a more suitable alternative (Janis 1995; Clauss et al. 2003, 2006; Sponheimer et al. 2003; Pérez-Barbería et al. 2004; Pérez-Barbería and Gordon 2005; Codron et al. 2007b; Hofmann et al. 2008). In our analysis here, we found that the mass of the masseter





**Fig. 2** Relationship between body mass and masseter muscle mass in 48 ruminant species (from Table 1) classified into three distinct feeding types. Slopes were similar for browsers (solid black line) and grazers (dotted line) but not for intermediate feeders (solid grey line)



**Fig. 3** Relationship of the phylogeny-controlled body mass residuals of the masseter muscle mass with the percentage of grass in the natural diet of ruminant species

muscle increased with the estimated proportion of grass in the natural diet, when controlling for body size and phylogeny.

However, getting reliable estimates of the species-specific proportion of grass in the natural diet is not an easy task (Clauss et al. 2008). Such data mostly come from collations using a variety of methods and are from studies of varying reliability (Gagnon and Chew 2000); variations due to seasonality and locality are not taken into account; and

the data on the composition of the natural diet are mostly not taken directly from the population from which the individuals measured derived (but see Codron et al. 2008b). Therefore, any analysis combining datasets of different origin must be treated with appropriate caution.

Hendrichs (1965) demonstrated that the mass of the masticatory muscles represented more than 300% of the mass of the mandibles in carnivores but only about 240% in non-ruminant herbivores, with the evident conclusion that the cutting, tearing and mastication of flesh and bones requires stronger forces than that of plant material. For ruminant herbivores, this ratio was even lower at 130%. Although empirical data are lacking, it is generally assumed that in comparison to nonruminant herbivores, rumination “relaxes” the functional load on the masticatory apparatus, because a part of the masticatory activity is performed on material that has already been soaked in ruminal fluid and “softened” by ruminal fermentation processes (Fortelius 1985; Sanson 1989). Taking these differences between major animal groups as indicators of differences in function, we can also hypothesize that differences in masticatory muscle mass within one of these groups—the ruminants—does have functional relevance.

In ruminants, the masseter is the largest of the masticatory muscles, representing between 44 and 54% of the total weight of all masticatory muscles combined (Hendrichs 1965). Changes in masseter muscle mass should therefore have a distinct influence on the masticatory processes in a ruminant organism. Given the equation described in the results, we can calculate a theoretical difference between a species consuming 10% of grass and a species consuming 90% of grass in their natural diets to be 11, 25, 48, 91, 213 or 405 g at body masses of 20, 50, 100, 200, 500 or 1,000 kg, respectively. At any given body mass, a theoretical browser (10% grass) would have, according to the equation, approximately 80% of the masseter muscle mass of a theoretical grazer (90% grass). These differences appear to be large enough to result in actual differences in masticatory forces applied.

Experimental studies have shown that differences in resistance to chewing actually do exist between some forage classes. Trials in agricultural science indicated that legumes are less costly to diminish in particle size than grasses when tested mechanically (Paul and Mika 1981; unpublished data in Wilson and Kennedy 1996; Henry et al. 1997; Wilman et al. 1997) or in vivo by the mastication action of domestic ruminants (Moseley and Jones 1984; Waghorn et al. 1989; Wilman et al. 1997). This is also reflected in the longer time spent ruminating (per unit of forage intake) for grass as compared with legumes in domestic ruminants (Sudweeks et al. 1981; Wilman et al. 1997; data in Coleman et al. 2003). If a closer similarity is assumed between leguminous forages fed to domestic ruminants on the one hand, and browse material

ingested by free-ranging, browsing ruminants on the other hand (as opposed to grass forage), then these reports support the general concept of grazers needing a particularly strong masticatory apparatus. Van Soest (1994, p. 54) speculated correspondingly that free-ranging, grazing wild ruminants spend a higher proportion of their activity budget ruminating than browsing ruminants, but the available data allowed no convincing conclusion. The only systematic comparison of forage classes with respect to their physical “resistance” is the investigation of Cornelissen and Thompson (1997) on litter decomposition rates and their factors of influence. These authors demonstrated that graminoid monocots had a drastically higher leaf tensile strength, or tearing resistance, than herbaceous dicots; no other dicots were tested in that study; however, the authors cite unpublished data on unspecified tree foliage that had a tensile strength higher than the herbaceous dicots but still lower than the monocots tested.

Together with the laminar surface area of the omasum (Clauss et al. 2006) and the salivary gland mass (Hofmann et al. 2008), the masseter muscle mass represents the only soft tissue parameter for which a correlation with %grass has been demonstrated so far in statistical tests accounting for phylogenetic linkage. Additionally, Pérez-Barbería et al. (2004) showed that the capability to digest fibre was higher in captive wild ruminant species with higher %grass, independent of phylogenetic relationships. More detailed studies on the differentiation of ruminant feeding types appear as logical further steps: The relevance of dietary shifts between seasons (Codron et al. 2007a, b) needs to be investigated with respect to morphophysiological adaptations. As grinding of C4 grasses needs distinctively more force than that of C3 grasses (Caswell et al. 1973), possibly due to a greater percentage of bundle sheaths in C4 grasses (Heckathorn et al. 1999), a differential look at the grazer guild that accounts for the different grass types ingested appears warranted. Additionally, the evolutionary history of individual ruminant groups or species (Codron et al. 2008a; Hofmann et al. 2008), which might have led to different morphophysiological solutions to the same feeding niches, remains to be explored in detail.

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